

ON THE HOMOLOGIES OF THE BORDERS AND
SURFACES OF THE SCAPULA IN
MONOTREMES.

By J. T. WILSON, M.B., PROFESSOR OF ANATOMY, UNIV. OF
SYDNEY, AND W. J. STEWART MCKAY, M.B., B.Sc.

(Plate XXI.)

There is not yet anything like a complete consensus of opinion regarding the homologies of the borders and surfaces of the monotreme scapula ; and indeed some very discrepant views have been set forth by various anatomists.

We shall not enter upon a description of the bone in detail, since the accounts given in several of the works dealing with the subject are satisfactory enough, and several of them are accompanied by figures (see list of references). It is with regard to the interpretation of the parts of the bone that we propose to offer a few observations.

Our attention was directed to the subject during the course of an investigation by one of us (M.) into the myology of the shoulder region in *Ornithorhynchus* and *Echidna*, the results of which will be published shortly.

Ever since Owen (1) the *actual* anterior margin of the monotreme scapula [‘margo anterior’ of Meckel (2) ; ‘bord antérieure’ of Cuvier (3)] has been generally recognised as the representative of the free margin of the mesoscapula, *i.e.*, as the free border of an anteriorly projecting scapular spine. This interpretation has at least been adopted by Flower (and Gadow) (4) and by Mivart (5), and it is in our view undoubtedly correct, being well supported by a study of the muscular attachments.

Giebel, however, in Bronn's 'Thier-Reich' (6) simply notices this border of the bone as a straight 'anterior' border, while, in his "Zootomie aller Thierklassen," Brühl (7) not only figures it merely under the latter name, but even designates the ridge running dorso-ventrally on the outer aspect of the scapula of *Echidna* as "die bei *Echidna* deutliche Spina"!

The true representative of the anterior or coracoid costa of the typical mammalian scapula was identified by Owen (1) in *Ornithorhynchus* with a ridge running dorso-ventrally on the 'inner' aspect of the bone. Along the line of this ridge the actual anterior part of the bladebone is flexed outwards so as to produce a marked hollowing of the whole outer surface. Dorsally the ridge begins close to the mesoscapular margin, but it inclines backwards as it passes ventrally and terminates, at the inferior or ventral extremity of the bone (glenoid region), near to the base of the acromion.

Except for this ridge the prescapula is totally suppressed. That area of the inner surface of the bone extending from the ridge in question to the free 'anterior' mesoscapular margin seems to represent that portion of the prescapular fossa which is ordinarily formed by the mesoscapula. And the opposite or 'outer' aspect of this same portion of the blade forms part of the wall of the postscapular fossa, giving origin to fibres of the infraspinatus muscle, which extends forwards as far as the mesoscapular margin. The posterior limit of the postscapular fossa is indicated by a distinct ridge, to which the scapular triceps is attached, and of which more anon.

It seems strange that Flower and Gadow (*loc. cit.*) should completely ignore the well-marked *prescapular* ridge on the inner aspect of the scapula of *Platypus*; especially as Owen (*loc. cit.*) so distinctly drew attention to it as the true 'anterior costa.' But the omission is possibly to be explained by the fact that, in their remarks on the monotreme scapula, the authors referred to seem to have had regard more particularly to the structure of the scapula in *Echidna* (which alone they figure); and in this it is to

be admitted the prescapular ridge is not represented by any recognisable mark. According to Owen (*loc. cit.*) it is "nearly obsolete" in *Echidna*. We hope to show, however, that, notwithstanding the absence of a distinct prescapular ridge, the condition in *Echidna* (as regards muscular attachments, &c.) does so essentially resemble that in *Ornithorhynchus* that it is an exceedingly simple matter to homologise the parts in the two genera. And if we interpret the ridge on the inner surface of the scapula of *Ornithorhynchus* (after Owen) as the true morphological anterior border (prescapular), it becomes comparatively easy to exhibit the real correspondence of the borders and surfaces of the scapula in monotremes to those in the typical mammalian scapula.

The identification of an area of the 'outer' surface of the scapula, by reason of its giving origin to the infraspinatus muscle, as 'postscapular fossa,' has already been alluded to. In *Ornithorhynchus* this postscapular 'fossa' extends from the actual anterior (true mesoscapular) margin of the bone as far back as the ridge already referred to as giving attachment to the scapular triceps. The like is true also of the scapula in *Echidna*, but here the tricipital ridge does not lie so far back as it does in the Platypus, but is separated by a considerable interval from the actual hinder border of the bone. In fact the 'outer' surface of the scapula in *Echidna* is nearly bisected into preaxial and postaxial halves by the tricipital ridge, which is more strongly marked than in *Ornithorhynchus*.

It may now be asked how the mode of attachment of the supraspinatus muscle agrees with the view so far expressed respecting the homologies of the parts of the bone. Naturally we should expect to find it associated with that part of the bone which represents the region of the prescapular fossa; and this, it will be remembered, we regard as that area of the inner surface of the scapula in *Ornithorhynchus* which lies between the *actual* anterior (mesoscapular) border and Owen's 'true anterior costa,' *i.e.*, the ridge formerly described. But the supraspinatus in *Ornithorhynchus* is a relatively very minute muscle, and it does not by any means occupy the whole of the above area. Its origin is

restricted to an exceedingly small portion of the bone close to the glenoid region and near to the root of the acromion. The *prescapular* ridge indeed fades away ere it reaches the origin of the supraspinatus, but its faint continuation towards the coracoid passes behind the muscle, which is thus situated to its acromial or mesoscapular side, as one would naturally expect.

Immediately above (dorsad of) the origin of the small supraspinatus is the attachment of another small muscle, the omohyoid, quite close to the continued prescapular line. The greater part of the 'prescapular fossa' is, however, occupied by portions of the attachments of the serratus magnus and acromiotrachelien muscles, which have, as it were, encroached upon the domain of the supraspinatus.

The area of the 'inner' surface of the scapula posterior to (*i.e.*, caudad of) the prescapular line (in *Ornithorhynchus*) is covered by part of the subscapularis muscle, fibres of which arise from the major part of it. The origin of this muscle reaches backwards to the actual posterior margin of the bone, and, further, extends around this upon the 'outer' aspect.

In *Echidna* the condition of the 'inner' surface of the scapula as to muscular attachments is, superficially, a very different one; and it is this fact which has probably largely helped to render the interpretation of the monotreme scapula more obscure. As stated above, there is in *Echidna* no recognisable prescapular ridge corresponding to that in *Ornithorhynchus*. At the same time, the supraspinatus muscle is relatively a very much larger muscle, whose origin occupies a very considerable area of the 'inner' surface of the bone, viz., nearly the whole of the inferior or ventral half of the surface above the glenoid region. As in *Ornithorhynchus*, the narrow attachment of the omohyoid muscle is placed immediately dorsad of it, in this case crossing the inner surface antero-posteriorly. The dorsal moiety of the surface, amounting to fully one-half of the 'inner' surface of the bone, is in large part bare of actual muscular attachment; but, dorsally, the insertion of the serratus magnus occupies it and extends far

ventralwards near both the anterior and posterior limits of the surface. As in *Ornithorhynchus*, the acromiotrachelien has an attachment close to the mesoscapular margin in front (cephalad) of the supraspinatus, and just ventral to the serratus magnus.

Thus it would almost appear as if nearly, if not quite, the entire 'inner' surface of the scapula in *Echidna* answered to that area in *Ornithorhynchus* included between the mesoscapular margin and the prescapular ridge, the *subscapularis* area of the inner surface in the latter animal being thus unrepresented. But this is not absolutely the case. For even in *Echidna* there is a narrow strip (as much as 3 mm. wide) of this same inner surface close to the actual posterior margin which is occupied by fibres of the subscapularis, though the major part of this muscle arises from the opposite ('outer') aspect of the bone. Plainly this posterior narrow subscapular strip of the inner surface corresponds to the broad subscapularis area of the 'inner' surface of the Platypus scapula which lies caudad of the prescapular ridge. We do not hold that it is necessary to suppose that the mere line of limitation between subscapularis on the one hand and supraspinatus on the other is the actual site of the morphological anterior border (prescapular ridge), but we do hold that either this is the case or, as is perhaps more likely, the absolute suppression in *Echidna* of any ridge marking the anterior costa has allowed of an encroachment by the supraspinatus upon the adjacent subscapularis area.

Flower (4), indeed, probably following Mivart [(5) p. 384], seems to imagine that the subscapularis in *Echidna* arises entirely from the 'outer' aspect of the scapula, and that it is limited behind by the posterior margin of the bone. Westling (9) also adopts this view.

Thus Mivart [(5) p. 398] states that in *Echidna* "the supraspinatus fossa is on the internal costal surface of the bone, and the infraspinatus is immediately behind its actual anterior margin. But," he continues, "while in *Ornithorhynchus* the subscapularis occupies that part of the internal or costal surface of the scapula which is not occupied by the supraspinatus, in the *Echidna*, on

the other hand, the subscapularis occupies exclusively the external surface of the scapula." And upon the strength of this view of the anatomy of *Echidna* Flower and Gadow accept the *actual* posterior margin of the scapula in the monotremes as the true morphological anterior costa or coracoid border.*

This view seems to us to be an erroneous one. The origin of the subscapularis even in *Echidna* not only occupies part of the 'outer' surface and the whole of the posterior border of the bone, but extends round it so as to occupy the narrow strip of the 'inner' surface aforesaid. And when we turn to the scapula of *Platypus* we find that the subscapularis area of the inner surface is so great as to include the major part of that surface. These considerations appear to us to vitiate a large part of Flower's interpretation of the monotreme scapula, which is based upon a mistaken view of the real condition in *Echidna*, and which fails to give due weight to the condition in *Ornithorhynchus*. But if we are to deny the homology of the actual posterior margin of the scapula to the true anterior or coracoid costa as suggested by Flower, in what light are we to regard the former?

Owen (1) simply accepts it as the "posterior margin or costa," and, so far as we know, all authorities save Mivart and Flower and Gadow so regard it (*cf.* Giebel and Brühl, *loc. cit.*). Here, however, we agree with Flower and differ from Owen in taking as the true morphologically posterior, or glenoid, or postscapular

* In a passage on p. 402 of his Memoir (5) Mivart says of *Echidna* :— "In that animal I find no trace of a ridge on the inside of the scapula like that which, in *Ornithorhynchus*, separates the supraspinatus from the subscapularis; but the supraspinatus is, nevertheless, separated from the subscapularis by a very large lamella, which throws the last-mentioned muscle entirely to the outer side of the scapula, and is the only one developed except that separating the supra- from the infraspinatus." Thus it would appear as if Mivart also were inclined to regard the actual posterior margin in *Echidna* as morphologically the anterior; while in *Ornithorhynchus* the homologue to the latter would be Owen's 'anterior costa' ridge. But this theory supposes a very wide discrepancy between the condition of the scapula in the two genera.

margin, that ridge on the 'outer' surface of the scapula which is present in both the genera, though most strikingly evident in the *Echidna*. This ridge we have already referred to as the 'tricipital.' Mivart states [(5) p. 401] that it might be considered to correspond to the axillary margin of the scapula of an ordinary mammal.

Owen styles the subscapularis in *Ornithorhynchus* "a narrow muscle" and regards it as restricted to the 'inner' surface; whilst, as we have seen, Mivart and Flower regard it in *Echidna* as equally restricted to the 'inner' surface. We find that in both instances the description is inaccurate—as already indicated for *Echidna*—and, for *Ornithorhynchus*, in the fact that a great part of what Owen has taken for *teres major* arising from the hinder part of the outer surface of the bone is really part of the subscapularis. In the scapulæ in both forms, in short, the subscapularis arises from both 'inner' and 'outer' surfaces (the proportions differing much in the two cases), and from the whole of the *actual* posterior margin itself. The latter we are therefore disposed to look upon as constituting morphologically a mere exaggerated ridge—perhaps of the same nature as the prominent and strongly marked subscapular ridge close to the true glenoid border of the human scapula.*

That the morphologically posterior, glenoid, or postscapular border of the monotreme scapula is, as Flower believes, represented by the ridge upon the outer surface is testified to by its relation in the way of attachment to the scapular triceps as well as by its forming the true separation between the infraspinatus

* This idea has at least been harboured by Mivart in reference to the scapula of *Platypus*, for he holds that we may theoretically consider "that there is a plate developed opposite to that separating the supra- from the infraspinatus muscle, which, as it were, passes into the midst of the subscapularis, throwing the posterior part of it to the outside and on to the same surface as that occupied by the infraspinatus, while the rest of it is but very slightly separated from the supraspinatus." The view of the writers is simply that this theory of the nature of the posterior margin of the scapula is good for *both* forms of monotreme scapula.

and subscapularis muscles in the scapulæ of both the genera of the order.

But it is not alone in the Monotremata that a displacement of the true postscapular border on to the outer surface of the scapula seems to occur. In his account of the anatomy of the scapula of *Myrmecophaga tetradactyla* in Bronn's "Klassen und Ordnungen des Thier-Reichs," Giebel [(6) p. 408, pl. LXX. fig. 5] describes the second or postscapular spine in the following terms:—"Ihr fast parallel [to the mesoscapular spine] läuft eine zweite Gräte, *der eigentliche Hinterrand* [the italics are ours], hinter welchem aber die Platte des Schulterblattes noch beträchtlich erweitert ist." And the condition here described is common to many edentate forms [(6) pl. LXX. and (8) pl. XXI.-XXIII.] and is also very prominent in the marsupial *Notoryctes typhlops* (10). In these cases it is associated with a very great development of the scapular triceps. Thus in *Dasypus sexcinctus* Galton (11) describes the scapular triceps as the largest part of the muscle, and as arising from the "inferior or lesser spine of the scapula along the whole of its extent." He also found a part attached to the actual "axillary" border of the bone just posterior to the neck of the bone which he opined to be the representative of the human long head; but in view of all the facts, we cannot admit this to be so to the exclusion of the rest of the scapular fibres. Indeed, the fact is that where the postscapular spine is present the triceps is not usually confined to it alone but spreads backwards upon the flat surface of bone behind it as far as the actual posterior margin of the bone, from which also fibres generally arise.

This at least is the case in *Notoryctes*, as ascertained by one of us (W.), and apparently it is so also in *Chlamydophorus truncatus* (12), in which a postscapular spine is well developed and the scapular triceps is "enormous."

In *Orycteropus capensis* Humphry (13) simply describes a very extensive origin by three divisions from the "posterior costa"; but, as in this animal the postscapular spine rises from the external surface pretty close to the actual posterior border, there can be no doubt that the attachment of the large muscle actually

reaches as far as the ridge and is not confined to the actual posterior margin of the blade. Galton's description of the condition in this animal does not differ from Humphry's in any essential feature (14).

Many rodents also exhibit a similar though less notable post-scapular spinous development, as may be well seen in the genus *Arctomys* [(6) pl. LXXI. fig. 11, and (8) pl. XXIV. fig. 14].

If Giebel's interpretation of the postscapular spine in *Edentata* be correct, we can then bring the monotreme condition in this respect well into line with the latter, as may be seen from a comparison of the series of figures 5-8.*

If the views we have expressed are correct, then there can be little difficulty in homologising the two forms of monotreme scapula. In both forms the actual anterior border is meso-scapular. In both the prescapular part of the bone is suppressed, though in *Platypus* its site is still indicated by a ridge on the inner surface. In both scapulæ the actual posterior border is really secondary, being an exaggerated subscapular ridge, the subscapularis muscle taking origin both from the ridge itself and the bone on both sides of it. Finally, and as a consequence of the last character, the postscapular border is displaced outwards and exists as a mere 'tricipital' ridge upon the outer surface of the flat bladebone.

Figs. 5-8 diagrammatically illustrate the points just summarised.

* We have already casually referred to the extraordinary view propounded by Brühl (7) that the postscapular ridge in question (tricipital) is "die bei *Echidna* deutliche Spina." In *Ornithorhynchus* he less confidently suggests a like view of the corresponding ridge. This theory not only ignores Owen's view (accepted by Flower) of the true spinous (mesoscapular) character of the actual anterior margin, but reveals either an entire ignorance of the muscular attachments of the scapula or a very extraordinary method in their interpretation. Thus in *Echidna* he suggests that the surface in front of this (tricipital or postscapular) ridge is a prespinous fossa, possibly homologous to the supraspinous fossa of higher mammals. But it is this very area which is occupied by the origin of the infraspinatus muscle; while the area behind the same ridge, regarded by Brühl as postspinous and possibly homologous to the infraspinous region, is occupied by part of the subscapularis muscle.

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EXPLANATION OF FIGURES.

PLATE XXI.

Each of the figures 1-4 has a key-sketch 1a-4a, showing the outlines of the muscular attachments.

The outlines of muscular attachments were drawn after careful examination of several specimens.

In figures 3a and 4a the partly broken off suprascapular part of the specimen, from which figures 3 and 4 were drawn, has been traced in.

Fig. 1. —Scapula (left) of *Ornithorhynchus*, internal aspect (nat. size).

Fig. 1a.—Tracing from fig. 1, with outlines of muscular attachments filled in.

Fig. 2. —Scapula (left) of *Ornithorhynchus*, external aspect (nat. size).

Fig. 2a.—Tracing from fig. 2, with outlines of muscular attachments filled in.

Fig. 3. —Scapula (left) of *Echidna* (youngish specimen), internal aspect (nat. size).

Fig. 3a.—Tracing from fig. 3, with outlines of muscular attachments filled in.

Fig. 4. —Scapula (left) of *Echidna*, external aspect (nat. size).

Fig. 4a.—Tracing from fig. 4, with outlines of muscular attachments filled in.

Figs. 5-8.—Diagrammatic outlines of sections across long (dorso-ventral) axis of several forms of scapula.



Fig. 5.—Typical mammalian.

Fig. 6.—*Ornithorhynchus*.

Fig. 7.—*Echidna*.

Fig. 8.—*Myrmecophaga*.

Lettering thus in figs. 5-8 :—

A.—Mesoscapular border (spinous).

B.—Prescapular border (anterior or coracoid).

C.—Postscapular border (posterior or glenoid).

D.—Subscapular (?) ridge.

Lettering of figs. 1a-4a.

Ac. Tr.'—Acromio-trachelien insertion of dorsal part. *Ac. Tr."*—Acromio-trachelien insertion of ventral part. *Clav. Delt.*—Clavicular part of deltoid muscle, origin. *Inf. Sp.*—Infraspinatus origin. *O. H.*—Omo-hyoid. *Rb.'*—Rhomboid, ant. part. *Rb."*—Post. part. *Sc. Delt.*—Origin of scapular deltoid. *Ser. Mag.*—Ins. of cervical part of serratus magnus. *S. M. Cost.*—Ins. costal part. *Sb. Sc.*—Origin of subscapularis on 'inner' surface. *Sub Sc.*—Subscapular origin on 'outer' surface. *Sup. Sp.*—Origin of supraspinatus muscle. *T. Major.*—Teres major, origin. *T. minor.*—Teres minor, origin. *Triceps L. H.*—Scapular triceps, origin. *Trap.'*—Ant. part of trapezius. *Trap."*—Post. part of trapezius.

N.B.—Figs. 1-4 are from drawings from nature by Mr. G. H. Barrow.